J. Austral. Math. Soc. (Series B) 24 (1982), 160–170

EXCHANGE OF EQUILIBRIA IN TWO SPECIES LOTKA-VOLTERRA COMPETITION MODELS

K. GOPALSAMY[1]

(Received 10 December 1980; revised 3 August 1981)

Abstract

Sufficient conditions are obtained for the existence of a unique asymptotically stable periodic solution for the Lotka-Volterra two species competition system of equations when the intrinsic growth rates are periodic functions of time.

1. Introduction

Suppose an ecosystem is modelled by the following system of autonomous ordinary differential equations

$$\frac{dx_i(t)}{dt} = x_i(t)f_i\{x_1(t), x_2(t),\dots,x_n(t), \mu_1,\dots,\mu_m\} \tag{1.1}$$

where $\mu_1, \mu_2,\dots,\mu_m$ are certain parameters with values in a bounded closed subset Ω of the nonnegative cone in $\mathbf{R}^m$. We assume that (1.1) has an asymptotically stable steady state at $(x_1^*, x_2^*,\dots,x_n^*)$ where

$$x_i^* = x_i^*(\mu_1, \mu_2,\dots,\mu_m) \geqslant 0, \qquad (\mu_1, \mu_2,\dots,\mu_m) \in \Omega. \tag{1.2}$$

The parameters $\mu_1, \mu_2,\dots,\mu_m$ are usually considered to represent the effects of the environmental as well as the interspecific and intraspecific interactions. We ask the following question: if the parameters μ_1, $\mu_2,\dots,\mu_m$ are replaced by continuous periodic functions say $\beta_1(t), \beta_2(t),\dots,\beta_m(t)$, $t \in \mathbf{R}$ respectively with a common period ω where

$$\{\beta_1(t), \beta_2(t),\dots,\beta_m(t)\} \in \Omega \quad \text{for } t \in \mathbf{R}, \tag{1.3}$$

[1] School of Mathematics, Flinders University, Bedford Park, South Australia 5042.

is there a periodic solution $\{y_i(t), i = 1, 2, \ldots, n\}$ of (1.1) such that

$$\left.\begin{array}{l} y_i(t+\omega) = y_i(t) \\ \{y_1(t), y_2(t), \ldots, y_n(t)\} \in \mathbf{R}^n_+ \end{array}\right\} \quad \text{for } t \in \mathbf{R} \tag{1.4}$$

where $\mathbf{R}^n_+$ is the nonnegative octant of $\mathbf{R}^n$? If such a periodic solution exists and is asymptotically stable we will say that an exchange of equilibrium of (1.1) occurs.

Such a problem of exchange of equilibrium has recently been considered by Rosenblat [11] and Gopalsamy [6] where the periodic parameters $\beta_i(t)$, $i = 1, 2, \ldots, m$, are considered to be perturbations of the form

$$\beta_i(t) = \mu_i + \varepsilon p_i(t), \qquad i = 1, 2, \ldots, m, \tag{1.5}$$

ε being a perturbation parameter while $p_i(\cdot)$, $i = 1, 2, \ldots, m$, are periodic in t with a common period. In a number of articles, Cushing [4, 5] has investigated the dynamics of systems of the type

$$\frac{dy_i(t)}{dt} = y_i(t) f_i\{y_1(t), \ldots, y_n(t), \beta_1(t), \ldots, \beta_m(t)\} \tag{1.6}$$

by converting (1.6) into a problem of bifurcation for periodic solutions and identifying the average of one of the periodic parameters $\beta_1, \ldots, \beta_m$ as a bifurcation parameter. Recently Mottoni and Schiaffino [9] have investigated the behaviour of the Lotka-Volterra two species competition model with periodic coefficients and compared the behaviour with that of the corresponding "averaged" system.

We remark that in model ecosystems exchange of equilibria need not always occur as can be verified for a simple system of the form

$$\frac{dx(t)}{dt} = \gamma x(t)\{1 - x(t)\}; \tag{1.7}$$

if γ is a positive constant, all solutions of (1.7) with positive initial values are such that $x(t) \to 1$ as $t \to \infty$; if we replace γ by $a(t)$ where $a(\cdot)$ is a strictly positive valued continuous periodic function then all solutions of

$$\frac{dy(t)}{dt} = a(t) y(t)\{1 - y(t)\} \tag{1.8}$$

with positive initial values are such that $y(t) \to 1$ as $t \to \infty$. Thus (1.7) does not possess the property of "exchange of equilibrium".

The existing literature on the theory of both autonomous and nonautonomous systems, including differential equations with periodic coefficients, does not answer the above mentioned question of "exchange of equilibrium" except when the periodicity involved is a perturbation of an autonomous case.

Recently Coleman [2] and Coleman *et al.* [3] have considered the logistic equation

$$\frac{dx(t)}{dt} = r(t)x(t)\{1 - x(t)/K(t)\} \tag{1.9}$$

where r and K are strictly positive continuous periodic functions with a common period. Boyce and Daley [1] have considered (1.9) with r a positive constant. By a change of the dependent variable in (1.9), one can solve explicitly the equation (1.9) for arbitrary r and K and, using such a technique, existence of a unique asymptotically stable periodic solution is established in [2] and [3]. Such an explicit solution is rarely possible for multispecies Lotka-Volterra model systems even in the case of constant coefficients.

2. A two species competition model in periodic environments

One of the classical models describing the dynamics of two species competing for a common supply of resources is described by a system of autonomous differential equations

$$\left.\begin{aligned} \frac{dx}{dt} &= x(b_1 - a_{11}x - a_{12}y) \\ \frac{dy}{dt} &= y(b_2 - a_{21}x - a_{22}y) \end{aligned}\right\}, \tag{2.1}$$

where it is usually assumed that b_i, a_{ij} $(i, j = 1, 2)$ are positive constants. If the intraspecific and interspecific coefficients satisfy the relation

$$a_{11}/a_{21} > b_1/b_2 > a_{12}/a_{22} \tag{2.2}$$

then it is known from phase plane techniques or from the method of Lyapunov functions that the solutions of (2.1) are such that

$$(x(t), y(t)) \to (\alpha, \beta) \text{ as } t \to \infty \quad \text{if } x(0) > 0 \text{ and } y(0) > 0 \tag{2.3}$$

where

$$\left.\begin{aligned} \alpha &= (b_1 a_{22} - b_2 a_{12})/(a_{11}a_{22} - a_{12}a_{21}) \\ \beta &= (a_{11}b_2 - a_{21}b_1)/(a_{11}a_{22} - a_{12}a_{21}) \end{aligned}\right\}. \tag{2.4}$$

Let us now suppose that the intrinsic growth rates b_1 and b_2 in (2.1) are strictly positive continuous periodic functions of time with a common period $\omega > 0$ so that

$$b_1(t + \omega) = b_1(t), \qquad b_2(t + \omega) = b_2(t) \quad \text{for } -\infty < t < \infty. \tag{2.5}$$

We will assume that the competitive interaction coefficients a_{ij} (i, $j = 1,2$) are positive constants; if some or all of a_{ij} are also strictly positive continuous periodic functions our analysis below can easily be modified to suit such a possibility. We will however assume in the following that a_{ij} (i, $j = 1,2$) are positive constants. Thus instead of (2.1) we will consider the periodic system

$$\left\{\begin{aligned} \frac{dx(t)}{dt} &= x(t)[b_1(t) - a_{11}x(t) - a_{12}y(t)] \\ \frac{dy(t)}{dt} &= y(t)[b_2(t) - a_{21}x(t) - a_{22}y(t)] \end{aligned}\right\} \tag{2.6}$$

and in the place of (2.2) we assume the following:

$$a_{11}/a_{21} > b_1^u/b_{2l}, \qquad b_{1l}/b_2^u > a_{12}/a_{22} \tag{2.7}$$

where

$$\left.\begin{aligned} \max_{-\infty<t<\infty} b_1(t) &= b_1^u > 0 \\ \min_{-\infty<t<\infty} b_1(t) &= b_{1l} > 0 \\ \max_{-\infty<t<\infty} b_2(t) &= b_2^u > 0 \\ \min_{-\infty<t<\infty} b_2(t) &= b_{2l} > 0 \end{aligned}\right\}. \tag{2.8}$$

One can consider (2.7) to be a generalization of (2.2) to the periodic case of (2.6). It is easy to see that the system (2.6) leaves the nonnegative quadrant $\{(x, y) \in \mathbf{R}^2 \mid x \geqslant 0,\ y \geqslant 0\}$ invariant and hence we have

$$\left.\begin{aligned} \frac{dx(t)}{dt} &\leqslant x(t)\{b_1^u - a_{11}x(t)\} \\ \frac{dy(t)}{dt} &\leqslant y(t)\{b_2^u - a_{22}y(t)\} \end{aligned}\right\} \quad \text{for } t \geqslant 0. \tag{2.9}$$

It follows from (2.9) that

$$\left.\begin{aligned} 0 < x(0) < b_1^u/a_{11} \\ 0 < y(0) < b_2^u/b_{22} \end{aligned}\right\} \Rightarrow \left.\begin{aligned} x(t) \leqslant b_1^u/a_{11} = x^u \\ y(t) \leqslant b_2^u/a_{22} = y^u \end{aligned}\right\} \quad \text{for } t \geqslant 0. \tag{2.10}$$

Similarly we derive

$$\left.\begin{aligned} \frac{dx(t)}{dt} &\geqslant x(t)\{(b_{1l} - a_{12}b_2^u/a_{22}) - a_{11}x(t)\} \\ \frac{dy(t)}{dt} &\geqslant y(t)\{(b_{2l} - a_{21}b_1^u/a_{11}) - a_{22}y(t)\} \end{aligned}\right\}. \tag{2.11}$$

As a consequence of (2.10) and (2.7) we derive

$$\left.\begin{aligned} x(0) > \frac{b_{1l}a_{22} - a_{12}b_2^u}{a_{11}a_{22}} = x_l \\ y(0) > \frac{b_{2l}a_{11} - a_{21}b_1^u}{a_{11}a_{22}} = y_l \end{aligned}\right\} \Rightarrow \left.\begin{aligned} x(t) \geqslant x_l \\ y(t) \geqslant y_l \end{aligned}\right\} \quad \text{for } t \geqslant 0. \tag{2.12}$$

We thus conclude that the rectangle $PQRS$ where

$$P = (x_l, y_l), \qquad Q = (x^u, y_l), \qquad R = (x^u, y^u) \quad \text{and} \quad S = (x_l, y^u) \tag{2.13}$$

is an invariant set for the nonautonomous periodic system (2.6). Such a rectangle lies in the interior of the nonnegative cone $\{(x, y) \in \mathbf{R}^2 \mid x \geqslant 0, y \geqslant 0\}$.

At this stage one can apply Theorem 2 of Massera [8] to assert the existence of periodic solutions of (2.6); since Massera's theorem does not provide uniqueness of the periodic solution and its stability, we will follow the method of concave operators below.

3. Existence of a periodic solution

Let us consider the system (2.6) in $\mathbf{R}^2$ with the norm in $\mathbf{R}^2$ being defined by

$$\|(x, y)\| = \max(|x|, |y|), \qquad (x, y) \in \mathbf{R}^2. \tag{3.1}$$

We know that when (2.7) holds there exists (for all finite values of t) a unique solution of (2.6) corresponding to every initial value $X_0 = (x_0, y_0) \in \mathbf{R}^2$; let such a solution be denoted by

$$X(t, X_0) = \{x(t, x_0, y_0), y(t, x_0, y_0)\} \quad \text{where } X(0, X_0) = X_0. \tag{3.2}$$

We define a shift operator also known as Poincaré's period map A: $\mathbf{R}^2 \to \mathbf{R}^2$ by the formula

$$AX_0 = X(\omega, X_0) \tag{3.3}$$

where ω denotes the period of the periodic functions b_1 and b_2 in (2.6). If one can show that the operator A has a fixed point say $X_0^* = (x_0^*, y_0^*)$ then it will follow that for the system (2.6) there is a solution $X^*(t)$ defined for $t \in [0, \omega]$ satisfying the condition

$$X^*(\omega) = X^*(0) = X_0^* \tag{3.4}$$

or equivalently

$$x^*(\omega, x_0^*, y_0^*) = x_0^*, \quad y^*(\omega, x_0, y_0) = y_0^*. \tag{3.5}$$

Since the right side of (2.6) is periodic in t with period ω, it will then follow that $X^*(t)$ can be extended for $t > \omega$ by periodicity in the sense that

$$X^*(n\omega + t) = X^*(t) \quad \text{for } n = 0, 1, 3, \ldots$$

for all values t and such an extension will be a solution of (2.6). Thus the existence of periodic solutions of (2.6) will follow from the existence of fixed points of the shift operator A defined above.

Since we are interested only in positive periodic solutions of (2.6) we will restrict the domain of definition of the operator A to a suitable subset of $\mathbf{R}^2$; usually the nonnegative quadrant

$$K_0 = \{(x, y) \in \mathbf{R}^2, x \geqslant 0, y \geqslant 0\}$$

will be considered. For our purposes this cone K_0 of nonnegative vectors of $\mathbf{R}^2$ is too big and we choose instead the following set $K \subset K_0$ where

$$K = \{(x, y) \in \mathbf{R}^2 \mid (x, y) = \lambda(u, v), (u, v) \in PQRS, \lambda \geqslant 0\}. \quad (3.6)$$

From our previous analysis we note that the shift operator A is positive with respect to the cone in the sense that $AK \subset K$.

The following result is well known.

THEOREM (Brouwer). *Suppose that a continuous operator U maps a closed bounded convex set $\Omega \subset \mathbf{R}^n$ into itself. Then Ω contains at least one fixed point of U; that is there exists at least one $z \in \Omega$ for which $Uz = z$ holds.*

THEOREM 1. *Suppose the conditions* (2.7) *hold for the system* (2.6). *Then* (2.6) *has at least one strictly positive periodic solution.*

PROOF. Consider the sets $\Omega_1 = \{(x, y) \in \mathbf{R}^2, (x, y) \in PQRS\}$ and $\Omega_2 = K$. The intersection $\Omega = \Omega_1 \cap \Omega_2$ is a closed bounded convex set in $\mathbf{R}^2$ and the operator A maps Ω into itself since the set Ω is invariant with respect to the system (2.6). This means that

$$(x_0, y_0) \in \Omega \Rightarrow \{x(t, x_0, y_0), y(t, x_0, y_0)\} \in \Omega \quad \text{for all } t \geqslant 0 \quad (3.7)$$

and hence $(x(\omega, x_0, y_0), y(\omega, x_0, y_0)) \in \Omega$ which implies that $A\Omega \subset \Omega$. The solution operator of (2.6) is continuous with respect to the initial values for all values of t from which the continuity of the operator A follows. Now by the Brouwer theorem the existence of at least one fixed point of A in Ω follows. Since such a fixed point has positive coordinates the corresponding periodic solution is strictly positive by the invariance of Ω.

To examine the uniqueness and stability of the periodic solution of Theorem 1 we introduce the following definitions.

DEFINITION 1. *An operator U: $D \subset \mathbf{R}^2 \to \mathbf{R}^2$ is said to be monotonic if $X_1 = (x_1, y_1) \in D$, $X_2 = (x_2, y_2) \in D$ and $X_1 < X_2$ in the sense $x_1 < x_2$, $y_1 < y_2$ implies $UX_1 < UX_2$.*

DEFINITION 2. *An operator U: $D \subset \mathbf{R}^2 \to \mathbf{R}^2$ is said to be positive with respect to a cone K in $\mathbf{R}^2$ if U: $K \to K$ and is said to be strictly positive if $UK \in$ interior of K.*

DEFINITION 3. *A positive operator U defined on a cone K in $\mathbf{R}^2$ is said to be strongly concave if for an arbitrary interior element $X \in K$ and any number $\tau \in (0, 1)$ there exists a positive number η such that*

$$U(\tau X) \geqslant (1 + \eta)\tau UX. \tag{3.8}$$

THEOREM 2. *The shift operator A corresponding to (2.6) and (2.7) is monotonic, strictly positive and strictly concave with respect to the cone K; A cannot have more than one fixed point in K and the corresponding periodic solution is uniformly asymptotically stable.*

PROOF. A set of sufficient conditions have been derived by Krasnoselskii [Theorem 10.2 of [7], p. 204] for the shift operator A of systems of the form (2.6) to be monotone, strictly positive and strictly concave with respect to the cone K. Since the cone K is narrower than K_0, positivity of A and strict positivity of A are equivalent on K. Since $X_0 \in K$, $X_0 \neq (0,0)$ implies that the components of X_0 are positive and hence $X(\omega, X_0) = AX_0 \in$ interior of K. If we rewrite the system (2.6) in the form

$$\frac{dx}{dt} = f_1(t, x, y), \qquad \frac{dy}{dt} = f_2(t, x, y), \tag{3.9}$$

then a sufficient condition for the monotonicity and strict concavity of A is that the functions F_1 and F_2 defined by

$$\left.\begin{aligned} F_1(t, \eta_1, \eta_2) &= f_1(t, \eta_1, \eta_2) - \left[\eta_1 \frac{\partial f_1(t, \eta_1, \eta_2)}{\partial \eta_1} + \eta_2 \frac{\partial f_1(t, \eta_1, \eta_2)}{\partial \eta_2}\right] \\ F_2(t, \eta_1, \eta_2) &= f_2(t, \eta_1, \eta_2) - \left[\eta_1 \frac{\partial f_2(t, \eta_1, \eta_2)}{\partial \eta_1} + \eta_2 \frac{\partial f_2(t, \eta_1, \eta_2)}{\partial \eta_2}\right] \end{aligned}\right\}, \tag{3.10}$$

are strictly positive in the sense that

$$\left.\begin{aligned} F_1(t, \eta_1, \eta_2) > 0 \\ F_2(t, \eta_1, \eta_2) > 0 \end{aligned}\right\} \quad \text{for } 0 < \eta_1, \eta_2 < \infty \text{ and } t \geqslant 0. \tag{3.11}$$

A direct verification of the conditions (3.10)–(3.11) for (2.6) reveals that the periodic operator A is strictly concave. It is known by Theorem 10.1 of Krasnoselskii [7] that A cannot have more than one fixed point in K and hence the periodic solution corresponding to the fixed point of A is unique; the uniform asymptotic stability of the unique periodic solution follows now by Theorem 10.6 of Krasnoselskii [7].

We conclude with a comment that the existence of unique asymptotically stable periodic solutions of ecosystems has some relevance to natural selection and evolution particularly to the way a species will utilise the resources and optimise its reproductive strategies. For more details of this aspect we refer to Boyce and Daley [1] and Nisbet and Gurney [10].

4. An example

The following example has been numerically solved for different initial conditions and the solutions are graphically illustrated in Figures 1, 2, 3, 4, 5.

$$\left.\begin{aligned} \frac{dx}{dt} &= x[2 + \sin \pi t - 2x - y] \\ \frac{dy}{dt} &= y[4 + \cos \pi t - x - 6y] \end{aligned}\right\}. \tag{4.1}$$

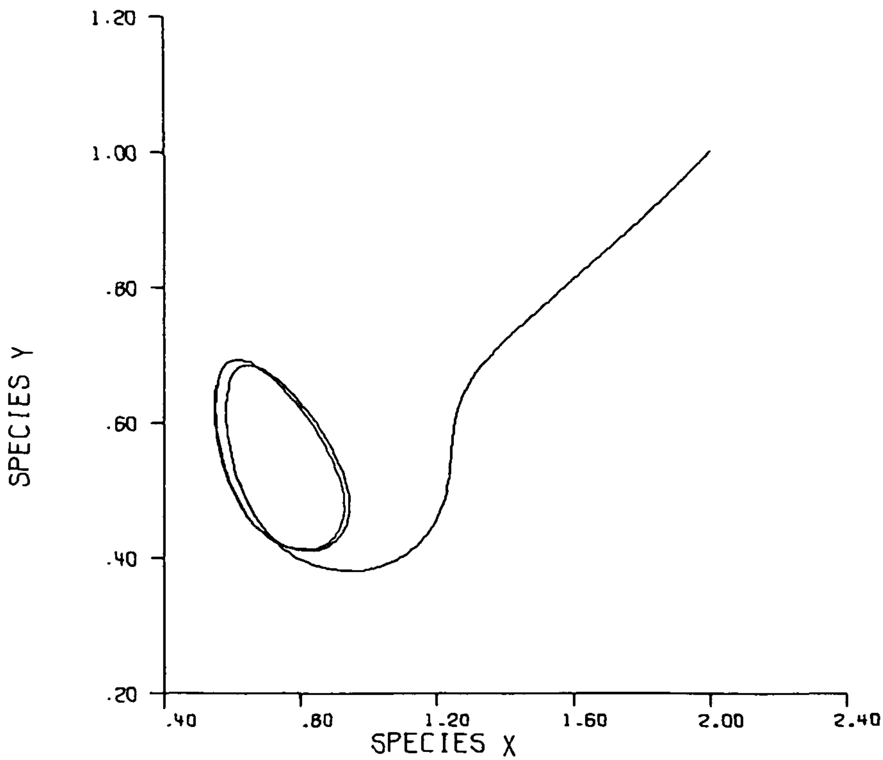

Figure 1. The solution of (4.1) with the initial conditions $(x(0), y(0)) = (2.0, 1.0)$.

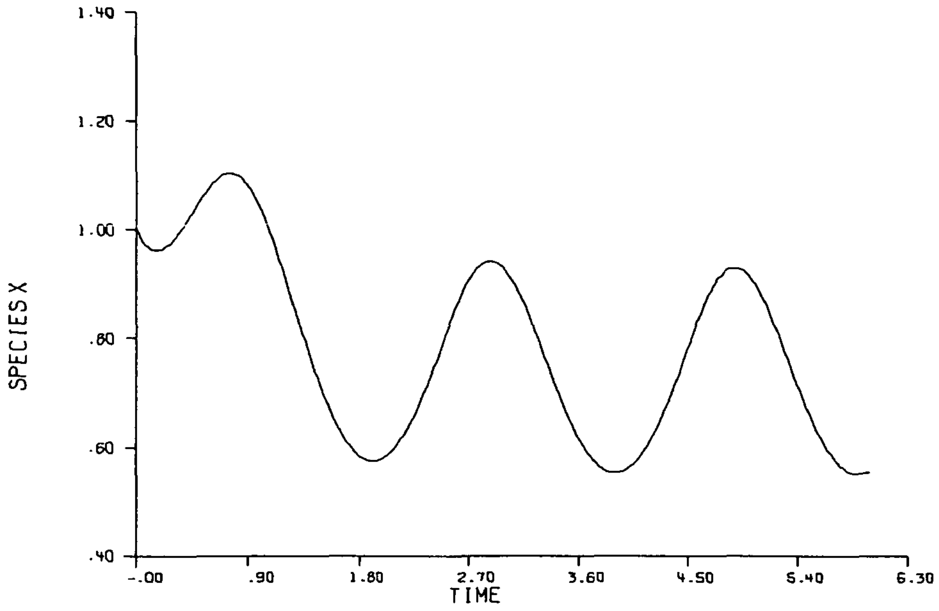

Figure 2. The value of x as a function of t for the system (4.1) subject to the initial conditions $(x(0), y(0)) = (1.0, 2.0)$.

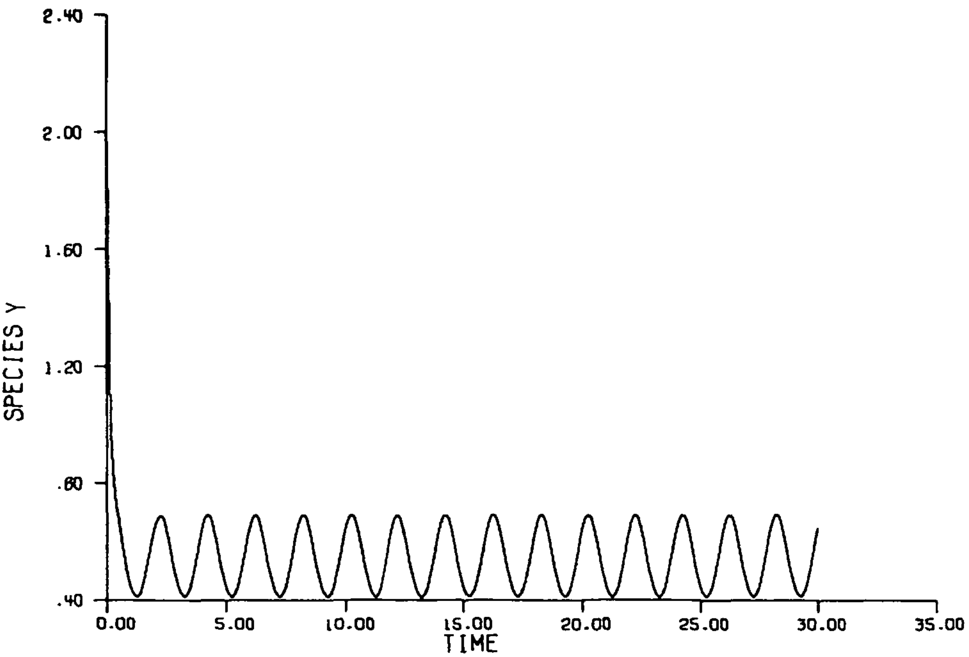

Figure 3. As for Figure 2 showing y as a function of t.

https://doi.org/10.1017/S0334270000003659 Published online by Cambridge University Press

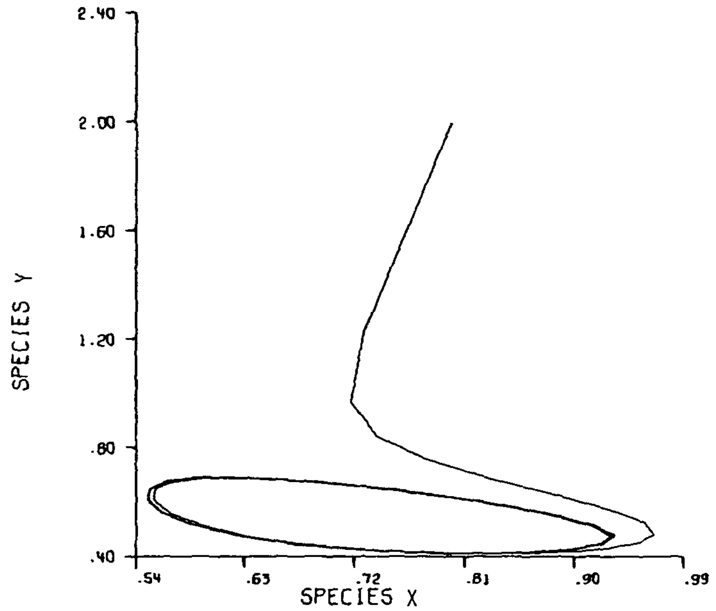

Figure 4. As for Figure 1 with $(x(0), y(0)) = (0.8, 2.0)$.

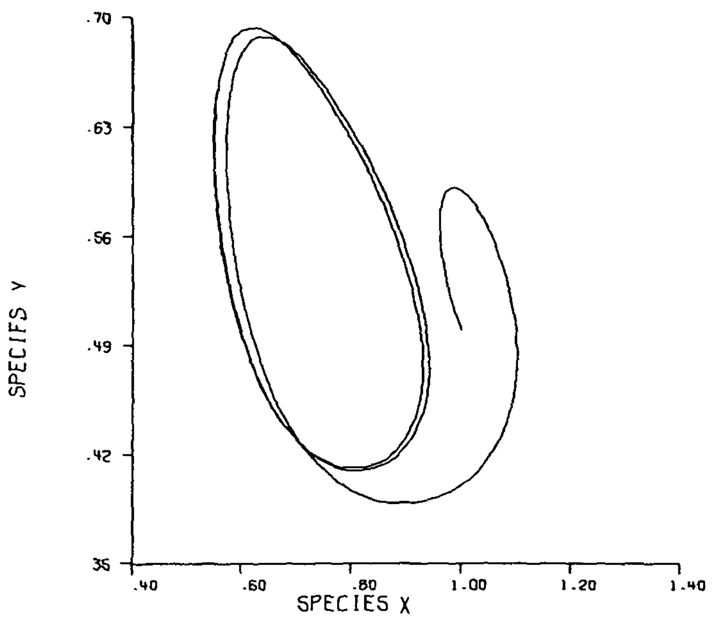

Figure 5. As for Figure 1 with $(x(0), y(0)) = (1.0, 0.5)$.

https://doi.org/10.1017/S0334270000003659 Published online by Cambridge University Press

References

[1] M. S. Boyce and D. J. Daley, "Population tracking of fluctuating environments and natural selection for tracking ability", *Amer. Natur.* 115 (1980), 480–491.

[2] B. D. Coleman, "Nonautonomous logistic equations as models of the adjustment of populations to environmental change", *Math. Biosci.* 45 (1979), 159–173.

[3] B. D. Coleman, Y. H. Hsieh and G. P. Knowles, "On the optimal choice of r for a population in a periodic environment", *Math. Biosci.* 46 (1979), 71–85.

[4] J. M. Cushing, "Periodic time-dependent predator-prey systems", *SIAM J. Appl. Math.* 32 (1977), 82–95.

[5] J. M. Cushing, "Two species competition in a periodic environment", *J. Math. Biol.* (to appear).

[6] K. Gopalsamy, "Limit cycles in periodically perturbed population systems", *Bull. Math. Biol.* (to appear).

[7] M. A. Krasnoselskii, "Translation along trajectories of differential equations", *Amer. Math. Soc. Transl.* 19 (1968).

[8] J L. Massera, "The existence of periodic solutions of differential equations", *Duke Math. J.* 17 (1950), 457–475.

[9] P. de Mottoni and A. Schiaffino, "Competition systems with periodic coefficients: a geometric approach", (to appear).

[10] R. M. Nisbet and W. S. C. Gurney, "Population dynamics in a periodically varying environment", *J. Theoret. Biol.* 56 (1976), 459–475.

[11] S. Rosenblat, "Population models in a periodically fluctuating environment", *J. Math. Biol.* 9 (1980), 23–36.